

Asymmetrical Effects of Introduced Bullfrogs (*Rana catesbeiana*) on Native Ranid Frogs in Oregon

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Introduced American Bullfrogs (*Rana catesbeiana*) have become widely established in the Pacific Northwest over the last century and are thought to be an important predator of native amphibians throughout the western United States. The Northern Red-Legged Frog (*Rana aurora aurora*) and Oregon Spotted Frog (*Rana pretiosa*) historically coexisted in portions of the Pacific Northwest now invaded by *R. catesbeiana*, but *R. pretiosa* has declined more severely than *R. a. aurora*. We investigated whether microhabitat and behavioral differences that facilitate sympatric coexistence of the natives predict which species is more susceptible to predation by introduced *R. catesbeiana*. Our laboratory experiments demonstrate that *R. catesbeiana* adults prefer aquatic microhabitats, that *R. pretiosa* juveniles are more aquatic than *R. a. aurora*, and that adult *R. catesbeiana* consume more *R. pretiosa* than *R. a. aurora* juveniles. Mean and maximum jump distances of *R. pretiosa* were shorter than equally sized *R. a. aurora*, and the difference between these two species increased with larger frog sizes. Our examination of field survey data indicates that *R. pretiosa* coexist with *R. catesbeiana* less frequently than *R. a. aurora*. We conclude that *R. catesbeiana* is a greater threat to survival of *R. pretiosa* than to *R. a. aurora* and suggest that microhabitat use and escape abilities of native ranid frogs may be linked to this asymmetrical effect. Analysis of behavioral and microhabitat differences among related native species may be a useful tool in predicting the effects of introduced predators on amphibians and can assist in developing conservation priorities for these species.

INVASIONS by nonindigenous species represent one of the primary threats to native aquatic biodiversity (Fisher and Shaffer, 1996; Richter et al., 1997; Mack et al., 2000). Increasingly important applications of contemporary ecology are to better predict the impacts of invasions, to identify which native species within invaded communities may be most at risk, and to identify the behavioral, life historical, and environmental attributes that mediate these impacts (Parker et al., 1999; Mack et al. 2000). Interactions between native and introduced aquatic fauna may be mediated by many factors, including differential temporal and spatial use of resources and predator evasion behaviors (Hill and Lodge, 1999; Kiesecker et al., 2001).

Native to North America east of the Great Plains, *Rana catesbeiana* is established throughout much of western North America and has also been introduced in Asia, Brazil, Europe and the Caribbean (Nussbaum et al., 1983; Stumpel, 1992; R. B. Bury and J. A. Whelan, U.S. Department of Interior, Resource Publication 155, Washington, DC). Because of its large body size, broad diets, and population densities that are frequently high, *R. catesbeiana* has potential to impact a variety of native species through predation and competition (Rosen and Schwalbe, 1995; Kiesecker and Blaustein, 1998).

The establishment of *R. catesbeiana* has been proposed as a factor in the declines of ranid frogs native to the western United States, including the Foothill Yellow-Legged Frog, *R. boylei* (Moyle, 1973; Kupferberg, 1997), California Red-Legged Frog, *R. a. draytonii* (Moyle, 1973; Lawler et al., 1999), Oregon Spotted Frog, *Rana pretiosa* (Dumas, 1966; Nussbaum et al., 1983), Northern Red-Legged Frog, *R. a. aurora* (Nussbaum et al., 1983; Kiesecker et al., 2001), and members of the *Rana pipiens* complex (Hammerson, 1982; Clarkson and Rorabaugh, 1989).

Rana catesbeiana is an important structuring agent in anuran communities in their native range (Werner et al., 1995; Hecnar and M'Closkey, 1997), but its effects on native *Rana* in the West have been difficult to elucidate (Hayes and Jennings, 1986; Adams, 1999). Recent investigations have been limited to *R. catesbeiana* interactions with native larvae (Kupferberg, 1997; Lawler et al., 1999; Kiesecker et al., 2001). Interactions between *R. catesbeiana* and native frogs are not limited to larval stages in the field, and predation on postmetamorphic anurans is likely to have proportionally greater population effects than larval interactions (Hellriegel, 2000; Biek et al., 2002; Vonesh and de la Cruz, 2002). Moreover, metamorphic and young juvenile anurans are the stages most vul-

nerable to predators (Arnold and Wassersug, 1978; Berven, 1990). These stages can represent a substantial portion of *R. catesbeiana* diet in both native and introduced ranges (Cohen and Howard, 1958; Stewart and Sandison, 1972; McAlpine and Dilworth, 1989). Predation on native juveniles could result in population-level effects, but experimental analyses of such interactions have not been preformed.

Rana aurora aurora and *R. pretiosa* historically coexisted in lowland lentic habitats from British Columbia through western Oregon, a region that has been colonized by *R. catesbeiana* for over 70 years (Nussbaum et al., 1983). *Rana pretiosa* has been extirpated from approximately 70% of its native range in the Pacific Northwest, including the Willamette Valley in Oregon (McAllister et al., 1993; M. P. Hayes, Oregon Dept. of Fish and Wildlife Tech. Rpt., unpubl.). *Rana aurora aurora* remains relatively widespread in the region, and declines have not been well documented (Adams et al., 1998; Richter and Azous, 2000; but see Kiesecker et al., 2001). Differential morphology and use of aquatic and terrestrial microhabitats allow the two native *Rana* to minimize competition where they occur syntopically (Licht, 1971, 1986a,b). *Rana catesbeiana* juveniles and adults are highly aquatic (Stewart and Sandison, 1972; McAlpine and Dilworth, 1989; Werner et al., 1995) as is *R. pretiosa* (Dumas, 1966; Licht, 1974). This has led some to hypothesize that continued *R. catesbeiana* invasion will be more detrimental to *R. pretiosa* than *R. a. aurora* (Dumas, 1966; Licht, 1974). To investigate this hypothesis, we compared predation susceptibility, microhabitat preference, and escape mobility differences between the two native ranids in experimental arenas and examined *R. catesbeiana* coexistence with native frogs in the field.

MATERIALS AND METHODS

Laboratory experiments.—We used experimental arenas to investigate the following hypotheses. (1) Postmetamorphic *R. catesbeiana* use aquatic more than terrestrial microhabitats. (2) *Rana pretiosa* juveniles use aquatic microenvironments more than *R. a. aurora* juveniles. (3) *Rana catesbeiana* prey upon juvenile *R. pretiosa* more heavily than juvenile *R. a. aurora* when both native species are available. Structural complexity mediates this interaction. (4) *Rana aurora aurora* juveniles have longer maximum and mean jumps than equally sized *R. pretiosa* juveniles.

We conducted all but the escape mobility experiment (see Experiment 4) in circular livestock watering tanks (180-cm diameter, 60-cm

deep). Twelve tanks were arranged linearly in a greenhouse at the Environmental Protection Agency's Willamette Research Station, Corvallis, Oregon. All tanks were set on slightly sloping pallets such that the water/land interface divided the circular tanks into equally sized half-circles. A 1-cm diameter PVC pipe supplied each tank with well water at a steady drip, and a drain-pipe outflow (which extended 0.5-cm above the water surface) was used to maintain water levels. We hung opaque black polyethylene along one side of the tank row to screen the tanks from the observer. Tanks were oriented with the aquatic-terrestrial interface perpendicular to our direction of observation so that both habitats would be equally observable through windows (30 × 3 cm) cut in the polyethylene shield. When scoring positions of test animals, a single observer moved quietly between viewing windows to minimize detection by frogs. We rinsed tanks with well water and allowed them to air-dry between experiments. For the experiments described below that included cover as a treatment, we added 60 culms of reed canarygrass (*Phalaris arundinacea*) to half the tanks (randomly chosen). Culms were trimmed to similar lengths (mean length 126.7 ± 2.4 cm SE and diameter 3.6 ± 0.1 mm; *n* = 100) and were reused in experiments. Stems were spread at a uniform thickness across both the aquatic and terrestrial halves of each tank. All experiments were conducted in October 2000.

We collected *R. a. aurora* as eggs from a pond in the Oregon Coast Range 20-km southwest of Corvallis; *R. pretiosa* eggs came from Klamath Marsh and Sunriver, Oregon. *Rana catesbeiana* were not present at any of the sites where native species were collected. We collected *R. catesbeiana* from two wetlands near Corvallis. All test animals were raised at the Willamette Research Station. We raised native tadpoles in 75-liter glass aquaria and fed them Purina rabbit chow ad libitum. *Rana catesbeiana* were housed in 75-liter glass aquaria before and between experiments, and were provided crickets (*Acheta domestica*) and small goldfish until 48 h before trials when all food was removed. Native juvenile frogs were provided crickets up until 24 h before trials. We measured snout-vent length (SVL) on all *R. catesbeiana* and every fourth native frog for each trial to the nearest 0.5 mm with a plastic millimeter-ruler. We used native juveniles in the experiment that were comparable in SVL. Mass of all frogs was determined to nearest 1 g using a Mettler PE3000 digital balance. We used S-Plus 2000 (Mathsoft, Inc.)

TABLE 1. SIZES OF FROGS USED IN EACH EXPERIMENT.

Experiment	Species	Number tanks	Frogs per tank	Snout-vent length (mm; Mean \pm SD)	SVL Range (mm)	n (Number of frogs measured)
1. <i>R. catesbeiana</i> positions	<i>Rana catesbeiana</i>	6	1	109.8 \pm 14.7	73.0–153.0	6
2. Native positions	<i>R. a. aurora</i>	6	7	24.3 \pm 0.6	19.5–29.0	16
	<i>R. pretiosa</i>	6	7	23.7 \pm 0.7	20.0–28.5	14
	<i>R. catesbeiana</i>	6	1	87.2 \pm 7.4	70.0–112.0	6
3A. First predation trial	<i>R. a. aurora</i>	12	7	24.3 \pm 0.4	20.0–28.0	21
	<i>R. pretiosa</i>	12	7	25.3 \pm 0.4	22.5–30.5	21
	<i>R. catesbeiana</i>	12	1	98.7 \pm 9.0	70.0–153.0	12
3B. Second predation trial	<i>R. a. aurora</i>	12	7	24.7 \pm 0.3	22.0–28.0	21
	<i>R. pretiosa</i>	12	7	25.2 \pm 0.5	21.0–30.0	21
	<i>R. catesbeiana</i>	12	1	101.2 \pm 8.5	61.0–152.0	12
4. Jump test	<i>R. a. aurora</i>			24.6 \pm 0.4	22.0–28.0	19
	<i>R. pretiosa</i>			25.3 \pm 0.4	21.5–30.0	18

for all statistical analyses and set significance at $\alpha = 0.05$.

Experiment 1: Rana catesbeiana microhabitat selection in experimental arenas.—To ascertain whether *R. catesbeiana* prefer aquatic microhabitats in experimental settings, we observed single, randomly selected *R. catesbeiana* in six randomly selected tanks over 3.75 h (three tanks with cover, three without; Table 1). We carefully introduced test individuals at the land/water interface and allowed them to acclimate for 45 min. To allow scoring of frog positions along the aquatic-terrestrial gradient, we drew parallel lines every 10 cm from the water/land interface (the origin or zero line) with nontoxic permanent green ink. We scored *R. catesbeiana* positions (at each frog's snout) every 15 min relative to the land/water interface, resulting in 10 observations per individual and 60 observations total. Air temperature was 25 C, and water temperatures in test tanks were 17.5–18.5 C. Water depth at the deep end of the tanks was 11.2–15.7 cm (mean 13.6 cm \pm 0.6 SE). We pooled *R. catesbeiana* positions for each animal and expressed them as mean and 95% confidence intervals. We used two-tailed *t*-tests to determine whether *R. catesbeiana* position or the proportion of observations that were aquatic depended on cover.

Experiment 2: Native anuran microhabitat selection in the non-lethal presence of Rana catesbeiana.—To compare *R. pretiosa* and *R. a. aurora* microhabitat selection, we scored native juvenile positions in the nonlethal presence of one *R. catesbeiana*. We used cages (16.0 \times 16.0 \times 12.0 cm) constructed of plastic frames and nylon window screen to contain one *R. catesbeiana* per tank and allow chemical and visual predator cues.

One *R. catesbeiana* was randomly assigned to each of six tanks (Table 1). Caged *R. catesbeiana* were positioned in the middle of each tank 15.1 cm on the aquatic side of the water line (the mean observed position of *R. catesbeiana* in the absence of prey; see results of Experiment 1). Three randomly chosen tanks received cover. Maximum water depth at the deep end of the tanks averaged 13.2 \pm 0.9 cm (range 11.2–16.9).

To be positive of species identification from behind the blind, we affixed contrasting color paper patches (approximately 5-mm diameter) midway down the dorsal surface of native juveniles with quick-setting glue. We observed no signs of behavioral differences due to glued patches, nor did we observe any obvious health effects on juveniles after patch removal at the termination of the experiment. Sizes of native juveniles did not significantly differ between *R. a. aurora* and *R. pretiosa* (Table 1; two-tailed *t*-test, *t* = 0.696, *df* = 28, *P* = 0.492). No frogs were reused for Experiment 3.

We carefully introduced seven *R. a. aurora* and seven *R. pretiosa* juveniles into each tank and all frogs were allowed to acclimate for 45 min. At 20-min intervals for the following 2.5 h, we scored native frog positions for each tank. Native frog positions were scored for clearly visible juveniles (those not obscured by other frogs or canarygrass culms). We scored positions as (1) in water on aquatic half of tank, (2) atop drain-pipe in aquatic half of tank, (3) directly on the land/water interface, or (4) on terrestrial half of tank. *Rana catesbeiana* escaped from their cages in three of the six trials, at which point these trials were terminated. This resulted in six observations over 2 h for three tanks, and four, four, and three observations for the other three tanks, respectively. The air temperature

during the experiment was 25 C, and water temperature in all tanks was 17 C. We treated all observations as independent and used a χ^2 test to determine whether the two species used positions 1, 2, and 4 differently. We did not include observations of frogs on the land/water interface in the analysis because of a small sample size.

Experiment 3: Rana catesbeiana predation on native juveniles.—We examined predation by free-ranging *R. catesbeiana* on native juveniles in 12 experimental tanks on two separate dates (trials). For each trial, we introduced seven juveniles of each native species into the center of each tank. After 50–70 min acclimation, we introduced one *R. catesbeiana* into each tank (Table 1). Native juveniles were only used once. All *R. catesbeiana* were used in both trials except for one escapee (73 mm SVL) that was replaced with a new animal for the second trial (104 mm SVL; Table 1). The first trial was terminated 7.1 h after the *R. catesbeiana* were introduced, at which point we counted the remaining natives. Air temperature during the trial was 25 C, and water temperatures in the 12 tanks ranged from 15.0–15.5 C. Water depth at the deep end of the tanks was 13.3 ± 0.5 cm (range 10.9–16.9).

The second trial was terminated 7.0 h after *R. catesbeiana* were introduced. Air temperature was 24 C, and water temperature in all 12 tanks was 16 C. Water depth in the deep end of tanks was 12.2 ± 0.3 cm (range 10.7–14.1). We used a one-tailed paired *t*-test, using data averaged over both trials, to determine whether *R. pretiosa* survival was lower than *R. a. aurora* survival. Because each individual *R. catesbeiana* was used in both a cover and a no-cover trial (with one exception, Table 1), we conducted a two-tailed paired *t*-test to assess effects of cover on the difference in survival of the two native species. We used a linear regression to compare the number of natives consumed per gram of *R. catesbeiana* mass to species of native and size (g) of *R. catesbeiana*.

Experiment 4: Escape mobility of native ranids.—We compared escape mobility of the two native anurans in linear runway tests. The experimental runway was made of corrugated cardboard (70 × 20 × 13-cm high) and was sloped gently toward a pan (40 × 23 × 6 cm) filled with water and canarygrass culms. White paper covered the runway floor and was replaced for each tested animal. We randomly selected juvenile frogs ($n = 19$ *R. a. aurora*; $n = 18$ *R. pretiosa*) from the same pool used for later behavior trials. After measuring SVL and mass, we placed the test

frog in a Petri dish with food coloring for 2 min. We initiated tests by gently placing the frog at the end of the runway, followed by a quick motion and stomp on the ground behind the animal. We measured distances to nearest millimeter between the stains left by the vent end of the frog for each individual. Air temperature during the tests was 25 C. We used a two-tailed *t*-test to compare mean and maximum jump distances between the two natives. We regressed frog size against mean and maximum jump length with linear regressions and compared the regression slopes between native species using a *t*-test (Zar, 1999).

Field survey data comparison.—We compared coexistence of the two native ranid frogs with *R. catesbeiana* from several regional surveys (see citations in Table 2). Studies included in this analysis all used a combination of standardized trapping, dip-netting, and visual encounter surveys designed to determine ranid frog presence and breeding status (e.g., Crump and Scott, 1994). We surveyed 85 wetlands in the Willamette Valley, Oregon, for amphibian breeding during Spring 1999–2001 (CAP, MJA, and RBB, unpubl. data). This region was historically occupied by both *R. a. aurora* and *R. pretiosa* and now supports widespread *R. catesbeiana*. We sampled all wetlands twice within one year with visual encounter surveys, dip-netting, and aquatic funnel trapping (Crump and Scott, 1994; Adams et al., 1997). We include the results in our comparison of native coexistence with introduced *R. catesbeiana* in Table 2.

Rana aurora aurora remains relatively widespread in lower elevations, and most of this range is occupied by *R. catesbeiana*. Available data document *R. pretiosa* from only approximately 35 populations, a portion of which occupy habitats above the known elevation limits of *R. catesbeiana* or are isolated by large areas of unsuitable habitat for *R. catesbeiana* and thus are outside the range of *R. catesbeiana* influence. We did not include isolated or high elevation sites in our comparison, which should only make the analysis more conservative. We used Fisher's Exact test with Yates' Continuity correction to compare rates of coexistence between each native species and *R. catesbeiana* (Zar, 1999). We also compiled occurrence data for the subset of wetlands that historically supported both native ranids and qualitatively compare current *R. a. aurora* and *R. pretiosa* occupancy relative to invasion by *R. catesbeiana* (Table 3).

TABLE 2. NUMBER OF SITES WHERE NATIVE RANID FROGS COEXIST WITH INTRODUCED *Rana catesbeiana* IN THE PACIFIC NORTHWEST.

Region	Sites with native frog breeding	Sites with native frog and <i>R. catesbeiana</i>	Source
<i>Rana aurora aurora</i>			
Puget Trough, Washington	20	12	Adams et al., 1999
Puget Trough, Washington	14	2	Adams et al., 1998
Puget Trough, Washington	9	3	Richter and Azous, 2000
Willamette Valley, Oregon	40	29	CAP, MJA, and RBB, unpubl. data
Total	83	36	
<i>Rana pretiosa</i>			
Western and Central Oregon	13	2	M. P. Hayes, Oregon Dept. of Fish and Wildlife Tech. Rpt., unpubl.
Western Washington	4	1	McAllister et al., 1993; Watson et al., 2003; M. P. Hayes, pers. comm.
Southwest British Columbia, Canada	3	1	R. D. Haycock, Report to Min- istry of Environment, Brit- ish Columbia, Canada, un- publ.
Total	20	4	

TABLE 3. RECENT OCCURRENCE OF *Rana pretiosa*, *Rana aurora aurora*, AND *Rana catesbeiana* AT SITES WHERE THE TWO NATIVE RANID FROGS ARE KNOWN TO HAVE HISTORICALLY COEXISTED.

Site	<i>R. catesbeiana</i>	<i>R. a. aurora</i>	<i>R. pretiosa</i>	Source
Mountain Slough, British Colum- bia	No	Yes	Yes	R. D. Haycock, Report to Ministry of Environment, British Columbia, Canada, unpubl.
Seabird Island, British Columbia	No	Yes	Yes	R. D. Haycock, Report to Seabird Island First Na- tions, unpubl.
Black River, Washington	No	Yes	Yes	McAllister et al., 1993; Wat- son et al., 2003
Little Campbell River, British Co- lumbia	Yes	Yes	No	Licht, 1974; R. D. Haycock, Report to Greater Vancou- ver Regional District, Parks Departmental, unpubl.
Nicomen, Island, British Colum- bia	Yes	Yes	No	R. D. Haycock, Report to Ministry of Environment, British Columbia, Canada, unpubl.
Spanaway Marsh, Washington	Yes	Yes	No	McAllister et al., 1993; Adams et al., 1998
McFadden Marsh, Oregon	Yes	Yes	No	M. P. Hayes, Oregon Dept. of Fish and Wildlife Tech. Rpt., unpubl.; CAP, un- publ. data
Naval Radio Section Aldergrove, British Columbia	Yes	Yes	Yes	R. D. Haycock, Report to Dept. of National Defence, unpubl.

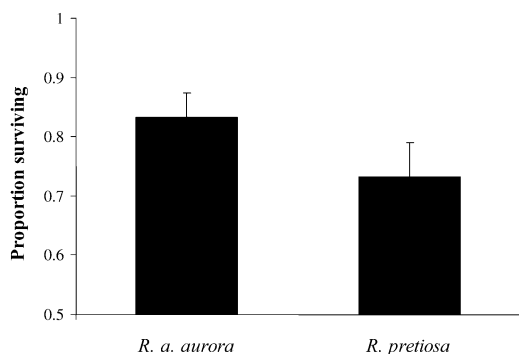


Fig. 1. Mean and SE of juvenile native frog survival per tank with free *Rana catesbeiana* predator ($n = 24$ tanks; one-tailed paired t -test, $t = 1.933$, $df = 11$, $P = 0.040$).

RESULTS

Experiment 1: *Rana catesbeiana* microhabitat selection in experimental arenas.—Of 60 observations on six *R. catesbeiana* in experimental arenas, most (73%) were in water on the aquatic half of the tank. The mean position was 15.1 cm on the aquatic side of the land-water interface (95% C.I. = 33.2 cm on aquatic side to 2.9 cm on terrestrial side). *Rana catesbeiana* positions did not differ significantly between cover treatments ($t = 0.076$, $df = 4$, $P = 0.943$). Proportion of *R. catesbeiana* observations in aquatic habitat did not differ significantly between cover treatments ($t = 2.121$, $df = 4$, $P = 0.101$).

Experiment 2: Native anuran microhabitat selection in the nonlethal presence of *Rana catesbeiana*.—We made 194 observations of *R. a. aurora* positions and 185 observations of *R. pretiosa* positions. The test of independence indicated that the use of aquatic, terrestrial, and drain-pipe habitats by the two species was different ($\chi^2 = 43.149$, $df = 2$, $P < 0.001$). *Rana aurora aurora* selected terrestrial positions in the arenas most often with 114 (58.8%) terrestrial observations, 6 (3.1%) observations at the land/water interface, 42 (21.6%) observations atop the drain-pipe, and 32 (16.5%) fully aquatic observations. Most *R. pretiosa* observations were also terrestrial, but a greater proportion was fully aquatic than was observed for *R. a. aurora*, and fewer *R. pretiosa* selected positions atop the drain-pipe: 114 (61.6%) terrestrial, 4 (2.2%) at the land/water interface, 1 (0.5%) atop the drain-pipe, and 66 (35.7%) fully aquatic.

Experiment 3: *Rana catesbeiana* predation on native juveniles.—When placed together in the experimental arenas with free *R. catesbeiana* predators,

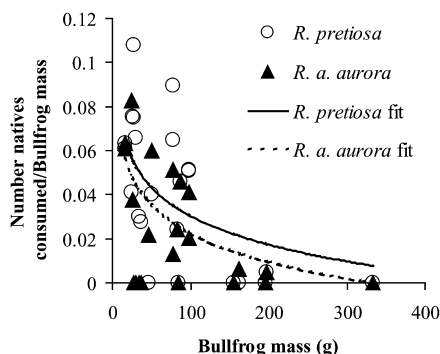


Fig. 2. Number of native ranid frogs consumed and size of *Rana catesbeiana* predator in 12 tanks. The best fitting regression model was Number of Natives Consumed/Mass = $0.108 + 0.008(\text{Species}) - 0.019[\ln(\text{Mass})]$ where Mass is the mass of *R. catesbeiana* (g) prior to the experiment and Species is 0 for *Rana aurora aurora* and 1 for *Rana pretiosa*. $R^2 = 0.36$.

R. a. aurora survived significantly better than *R. pretiosa* (*R. a. aurora* survival = 0.83 ± 0.05 , *R. pretiosa* survival = 0.73 ± 0.08 ; one-tailed paired t -test, $t = 1.933$, $df = 11$, $P = 0.040$; Fig. 1). In 10 of the 24 arenas, more *R. pretiosa* juveniles were consumed than *R. a. aurora*; in four arenas, more *R. a. aurora* were consumed than *R. pretiosa*, and in 10 arenas, equal numbers of the two natives were consumed. We did not find a significant effect of cover on the survival of natives (two-tailed paired t -test, $t = 0.89$, $df = 11$, $P = 0.393$). Smaller *R. catesbeiana* consumed more natives per bodyweight than did larger *R. catesbeiana* ($F_{1,45} = 21.195$, $P < 0.001$), and *R. catesbeiana* of all sizes consistently consumed more *R. pretiosa* than *R. a. aurora* ($F_{1,45} = 5.022$, $P = 0.030$; Fig. 2). Sizes of tested *R. a. aurora* and *R. pretiosa* were not significantly different in either the first (two-tailed t -test, equal variance, $t = -1.559$, $df = 40$, $P = 0.127$) or second trial ($t = -0.944$, $df = 40$, $P = 0.351$).

Experiment 4: Escape mobility of natives.—*Rana aurora aurora* exceeded *R. pretiosa* in mean (average difference between natives = 40.4 mm, $t = -3.106$, $df = 35$, $P = 0.004$) and maximum jumps (average difference = 38.0 mm, $t = -2.070$, $df = 35$, $P = 0.046$; Fig. 3). Frog size was a significant predictor of *R. a. aurora* mean (mean jump = $-108.158 + 9.869(\text{SVL})$; $r^2 = 0.26$, $F_{1,17} = 5.971$, $P = 0.026$) and maximum jumps (maximum jump = $-250.291 + 17.062(\text{SVL})$; $r^2 = 0.35$, $F_{1,17} = 9.011$, $P = 0.008$) but was not significant for *R. pretiosa* mean (mean jump = $-28.480 + 4.824(\text{SVL})$; $r^2 = 0.043$, $F_{1,16} = 0.713$, $P = 0.411$) nor maximum jumps (maximum jump = $-13.475 + 5.689$

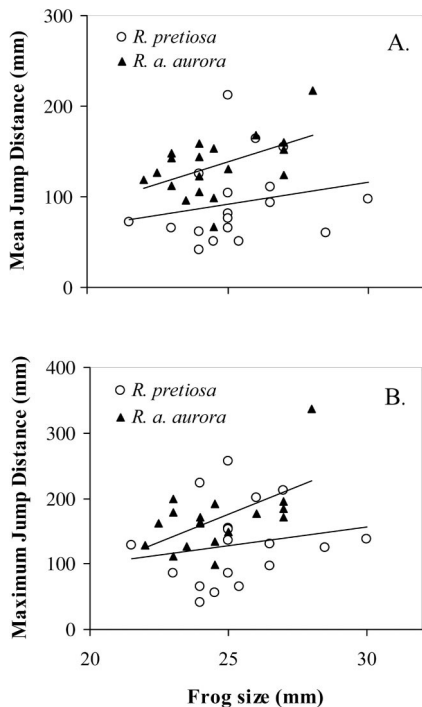


Fig. 3. Mean (A) and maximum (B) jump distances of juvenile *Rana aurora* and *Rana pretiosa* on runways in the laboratory.

(SVL); $r^2 = 0.032$, $F_{1,16} = 0.530$, $P = 0.477$). The slope of the relationship between jump distance and frog size was significantly greater for *R. a. aurora* than for *R. pretiosa* for both the mean ($t = -2.531$, $df = 33$, $P = 0.017$) and the maximum jumps ($t = 3.500$, $df = 33$, $P = 0.001$). Sizes of tested *R. a. aurora* and *R. pretiosa* were not significantly different ($t = -1.289$, $df = 35$, $P = 0.206$; Table 1).

Field survey data comparison.—Recent surveys have found breeding populations of *R. a. aurora* at 83 of 168 (49%) lentic sites in the Puget Trough (Adams et al., 1998, 1999; Richter and Azous, 2000) and Willamette Valley (CAP, MJA, and RBB, unpubl. data; Table 2). Extensive surveys have failed to detect *R. pretiosa* in the Willamette Valley (Nussbaum et al., 1983; M. P. Hayes, Oregon Dept. of Fish and Wildlife Tech. Rpt., unpubl.; CAP, MJA, and RBB, unpubl. data). *Rana catesbeiana* occurred syntopically with *R. a. aurora* at 46 sites (55%) examined in recent surveys. *Rana catesbeiana* occurred at four of the 20 *R. pretiosa* breeding sites (20%) in areas within the current range of *R. catesbeiana*. Coexistence was significantly less common between breeding *R. pretiosa* and *R. catesbeiana* than between *R. a. aurora* and *R. catesbeiana* at

these sites ($\chi^2 = 6.739$, $df = 1$, $P = 0.010$). Of those eight sites where *R. a. aurora* and *R. pretiosa* are known to have coexisted, five now support *R. catesbeiana*; *R. a. aurora* persists at all five sites (100%) now supporting *R. catesbeiana*, and *R. pretiosa* persists at one (20%) of those sites (Table 3). Both native *Rana* remain at the three sites that do not support *R. catesbeiana*.

DISCUSSION

Native *Rana* in the lowland Pacific Northwest have been exposed to *R. catesbeiana* since Bullfrog introduction in the region as early as the 1920s (Nussbaum et al., 1983). Both Dumas (1966) and Licht (1974) hypothesized that the spread of *R. catesbeiana* posed a particular threat to *R. pretiosa* caused by both species' aquatic habitat affinities. The hypothesis that *R. catesbeiana* are more detrimental to *R. pretiosa* than to *R. a. aurora* was supported by our laboratory experiments and review of field patterns of coexistence. Our laboratory studies demonstrate that postmetamorphic *R. catesbeiana* prefer aquatic microhabitats, a pattern that is also evident in field investigations in their native range (McAlpine and Dilworth, 1989; Werner et al., 1995). Consistent with field observations (Licht, 1986b), we found that *R. pretiosa* made greater use of fully aquatic positions than did *R. a. aurora*, which we believe increases probability of encountering aquatic *R. catesbeiana*. *Rana aurora* more commonly chose positions atop drain-pipes. Selection of elevated or terrestrial positions may afford improved visual detection of approaching aquatic predators and allow effective evasion by remaining immobile and relying on last-minute explosive leaps (Licht, 1986a; Heinen and Hammond, 1997).

We found that in our experimental arenas, *R. catesbeiana* consumed more *R. pretiosa* than *R. a. aurora* and that this asymmetry could be explained by native frog microhabitat preference and escape mobility. That the slope of the jump distance-to-size regressions for *R. pretiosa* was lower than for *R. a. aurora* suggests that even *R. pretiosa* larger than we tested would find it more difficult to escape *R. catesbeiana* by jumping than equally sized *R. a. aurora*. Although the sample size was small, our analysis of recent field surveys suggests a pattern of coexistence consistent with the hypothesis that *R. catesbeiana* are more detrimental to *R. pretiosa* than to *R. a. aurora* (Table 2).

Anurans can represent a large portion of adult Bullfrog diets (Stewart and Sandison, 1972; McAlpine and Dilworth, 1989; R. B. Bury and J. A. Whelan, U.S. Department of Interior,

Resource Publication 155, Washington, DC). Habitat overlap and escape ability are two factors that can influence anuran susceptibility to predators such as adult *R. catesbeiana* (Wassersug and Sperry, 1977; McAlpine and Dilworth 1989). Microhabitat preference and behavioral differences have been hypothesized to mediate *R. catesbeiana* effects on sympatric ranid frogs in southeastern Canada (Hecnar and M'Closkey, 1997) and garter snakes in the southwestern United States (Rosen and Schwalbe, 1995). We acknowledge that other interactions may also influence the distributions of *R. pretiosa* and *R. a. aurora* in the Pacific Northwest. For example, the aquatic habits of *R. pretiosa* may expose them asymmetrically to predation by nonnative fish that often coexist with *R. catesbeiana* (see Hayes and Jennings, 1986; Adams et al., 2003). Differences in competitive abilities of *R. pretiosa* and *R. a. aurora* larvae in the presence of *R. catesbeiana* are unknown but could also influence community structure.

Although the difference in survival of *R. pretiosa* and *R. a. aurora* in the presence of *R. catesbeiana* was relatively small in our experiment (mean *R. pretiosa* survival = 73.2%; mean *R. a. aurora* survival = 83.3%), several factors are likely to increase the importance of this difference in field conditions. First, elasticity analyses suggest that population dynamics of north-temperate anurans, including *R. a. aurora*, are most sensitive to changes in survivorship of the juvenile (metamorphosis to year 1) rather than the larval or adult stages (Biek et al., 2002). Thus, small changes in juvenile survivorship may have important implications for population trends over longer temporal windows. Second, *R. pretiosa* females lay fewer eggs per mass than *R. a. aurora*, and hatching rates are often lower in *R. pretiosa* in part because of their ovipositing in shallower water that exposes them to desiccation and freezing (Licht, 1974; Nussbaum et al., 1983). Other things being equal, *R. pretiosa* should recruit fewer juveniles per breeding female than *R. a. aurora*, making survivorship of those juveniles potentially more important to persistence of the population. Finally, *R. a. aurora* adults use terrestrial habitats more than adult *R. pretiosa*, and *R. a. aurora* juveniles disperse from breeding sites within days or weeks after transformation (Licht, 1974, 1986b). Conversely, *R. pretiosa* remain tightly linked to aquatic environments through their entire life history (Licht, 1974, 1986b), including the late summer when high densities of juvenile *R. catesbeiana* are concentrated as the pond dries. Our predation trials suggest that juvenile *R. catesbeiana*, which can attain exceptionally high densities in their

introduced range (Cohen and Howard, 1958), are capable of consuming substantial numbers of juveniles of both native ranids. That *R. pretiosa* experience longer potential exposure to *R. catesbeiana* at breeding sites than *R. a. aurora* may magnify the difference in short-term survival that we documented.

Continued introductions and the increasing availability of constructed permanent ponds used by *R. catesbeiana* suggest that the species will continue to expand its range in the western United States, as well as portions of Europe, Asia, and Latin America. The apparent differential effect of *R. catesbeiana* predation on natives has implications for other ranid frogs. Species such as *R. pretiosa* that are more aquatic throughout their life history and with relatively poor abilities to evade predators are more likely to be impacted. Examples may include several ranids of the southwestern United States, *R. chiricauhensis*, *R. subaquavocalis*, *R. yavapaiensis*, and *R. onca*, as well as *R. a. draytonii* (which is more aquatic than *R. a. aurora*). More broadly, traits that allow coexistence between related native species by segregating spatially or temporally may be useful in predicting effects of introduced species and directing conservation attention toward potentially susceptible native species.

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